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CROSSING OVER, NON-DISJUNCTION, AND MUTATION IN *DROSOPHILA VIRILIS*

PRELIMINARY REPORT OF WORK DONE ON THE SIGMA XI FOUNDATION

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Every individual contains in each cell of its body two full sets of chromosomes, one set derived from each parent. The modern study of genetics has produced strong evidence that these chromosomes are the carriers of the hereditary factors or genes.

In the formation of the eggs and sperm, the chromosomes first come together in pairs; then each chromosome separates from its mate and the two go to different cells, so that each egg or sperm receives only one chromosome of each pair. Hence an egg or sperm contains only one set of chromosomes instead of the two sets contained in each somatic cell.

When the two chromosomes of a pair separate, each carries its genes with it and these are inherited as a group. Sometimes, however, the chromosomes before separating interchange homologous pieces, so that the resulting chromosomes carry combinations of genes different from the combinations in the original chromosomes. This interchange of homologous sections of chromosomes is termed crossing over. It is obvious that, other things being equal, the longer a portion of a chromosome, the more likely is a break or crossing over to occur within it (Morgan). Therefore the frequency with which two genes undergo recombination furnishes an index of their distance apart; and by comparing the frequencies with which different genes undergo recombination it is possible to construct a map of the chromosome, showing the relative location of the genes within it. For convenience, a unit of map distance is taken to represent one per cent of crossing over. In such maps, the arrangement of genes in the chromosome turns out to be linear (Sturtevant).

CROSSING OVER IN *Drosophila virilis*

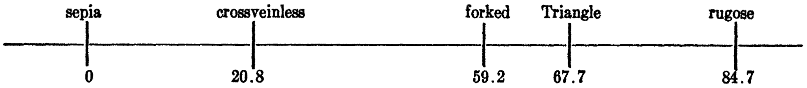
The study of crossing over throws light on both the make-up of the chromosomes and their behavior. With this in mind, I have

TABLE I

Females	*Males*																
	Non-crossovers	Single crossovers				Double crossovers						Triple crossovers				Quadruple crossovers	Total
		Region 1*	Region 2	Region 3	Region 4	1, 2	1, 3	1, 4	2, 3	2, 4	3, 4	1, 2, 3	1, 2, 4	1, 3, 4	2, 3, 4	1, 2, 3, 4	
12984	3195	933	2309	383	691	447	108	230	152	414	54	42	118	13	21	2	9112

*The figures in this row refer to the regions of the chromosome in which the crossing over has occurred, the regions being numbered from left to right; that is, sepia crossveinless is region 1, crossveinless forked is region 2, etc.

been studying crossing over in the X chromosomes of *Drosophila virilis,* using the factors sepia (eye color), crossveinless (venation), forked (bristles), triangle (venation), and rugose (eye). The location of these factors in the chromosome on the basis of their percentages of recombination in this experiment is shown in the accompanying map; the data themselves are given in Table 1. Of these factors, sepia, forked, and rugose were discovered and located by Metz (the sepia data have not yet been published); crossveinless was discovered and located by the writer. Triangle, which consists of a thickening of the cross-veins and of the ends of the longitudinal veins, is a partial dominant; it was discovered by Metz, and my data show that it is sex linked, its locus lying between forked and rugose, 8.5 units from forked and 16.9 units from rugose.



It has been said that the frequency of crossing over depends on the length of the region involved. The frequency is, however, known to be affected by other conditions. Thus, in the second chromosome of *Drosophila melanogaster,* crossing over decreases with increased age of the mother (Bridges) and increases with increase or decrease in temperature (Plough). The present experiments were all performed with flies raised at 25° C., so that if there is any temperature variation in *D. virilis,* the results represent the crossing over relations at this temperature. Most of the females were transferred to fresh culture bottles at the end of 10 days, and to a third set of bottles after 13 days more, so that three successive broods were available for comparison. The recombination percentages calculated for these broods separately, as well as for all the data together, are given in the following table.

TABLE 2

Region	*Brood 1*	*Brood 2*	*Brood 3*	*Total Data*
Sepia Crossveinless	20.80	21.13	20.30	20.78
Crossveinless Forked	38.13	39.56	37.96	38.47
Forked Triangle	8.47	9.04	8.32	8.51
Triangle Rugose	16.53	17.67	16.34	16.93

It is seen from this table that the variation in crossing over in successive broods is too small to be significant. This agrees with the situation in the X chromosome of *D. melanogaster*. The data in the table do not, however, necessarily prove that crossing over does not vary with age in *D. virilis;* for the values given are averages over rather long periods and it is possible that there was variation within each period. To test this point it is planned to transfer the females at two-day intervals so as to have a more accurate analysis of the situation. It is also planned to vary the temperature to find out whether such a change affects crossing over.

MULTIPLE CROSSING OVER AND COINCIDENCE

Crossing over may occur simultaneously at more than one point of a chromosome; thus an X chromosome of *D. virilis* might undergo crossing over both between sepia and crossveinless and between forked and Triangle. It has been found in *D. melanogaster* that for regions near together in a chromosome, crossing over in one region tends to prevent or interfere with crossing over in neighboring regions. In general, this interference decreases as the distance between the regions concerned becomes longer (Muller); but when the intermediate distance increases beyond a certain limit, interference increases again (Weinstein, Bridges, Gowen).

From this point of view it is of interest to study interference in *D. virilis,* particularly as the X chromosome in this species is genetically longer than in *D. melanogaster*. A measure of the interference is obtained by calculating the coincidence, which is done as in the following example. The amount of recombination for the sepia crossveinless region is about twenty-one per cent and for the forked Triangle region about nine per cent. If crossing over in one region neither helped nor hindered crossing over in the other, double crossing over involving both regions simultaneously would occur in nine per cent of twenty-one per cent of all the cases; that is, the double crossovers would amount to 1.9 per cent of all the individuals. In the present experiment the double crossovers do not come up to this expectation but amount to only 1.3 per cent of the total; that is, they are only three quarters as numerous as would be expected if there were no interference. This is expressed by saying that the coincidence is 0.75, which means that about 75 per cent of the double crossovers expected are realized. If we calculate the coincidence of the sepia crossveinless and Triangle rugose regions, we find the value to be 0.72. In this case a smaller proportion of the expected number of double crossovers has been realized. This suggests that, as in *D. melanogaster,* when the intermediate distance increases beyond a certain limit, interference increases.

Of course the difference in coincidence in the two cases is not very marked and the above conclusion is only tentative. But the conclusion is borne out by the coincidence of sepia crossveinless and crossveinless forked. Here the average distance between the breaking points in double crossing over is shorter than in the other cases, and the coincidence is higher; namely, 0.84. This coincidence, moreover, is a compound value. For since the crossveinless forked distance is very long, the coincidence of its different parts with sepia crossveinless is different, the regions near sepia crossveinless having a lower coincidence than those farther away. Consequently the region just to the left of forked must have a higher coincidence than the average for the entire region, and the decline of coincidence to the right of forked must be more marked than the figures given above would indicate. This is further borne out by a calculation previously made by the writer which indicated that the coincidence of yellow crossveinless and magenta forked is about 1.4, and the coincidence of yellow vesiculated and magenta forked about 0.99.

TABLE 3

THE VALUES OF COINCIDENCE AND THE AVERAGE DISTANCES BETWEEN BREAKING POINTS IN DOUBLE CROSSING OVER FOR THE VARIOUS REGIONS IN THE EXPERIMENT

Region	*Coincidence*	*Average distance between breaking points*
Sepia crossveinless and crossveinless forked	0.836	29.6
Sepia crossveinless and forked triangle	0.752	53.1
Sepia crossveinless and triangle rugose	0.718	65.9
Crossveinless forked and forked triangle	0.728	23.5
Crossveinless forked and triangle rugose	0.896	36.2
Forked triangle and triangle rugose	0.686	12.7

For double crossing over when the breaking points are near together, coincidence is again lower. This is shown in the present data by the coincidence of forked Triangle and Triangle rugose. Here the average distance between breaking points is only 12.7 and the coincidence is 0.69.

A consideration of the coincidence data given in Table 3 and of data previously published makes it probable that the most frequent distance between breaking points in double crossing over in *D. virilis* is about 47 (but this figure must be regarded as tentative). This agrees with the figure obtained for the X chromosome in *D. melanogaster,* where the distance was found to be about 46. The value obtained for *D. virilis* represents roughly half the length of the chromosome; hence if crossing over occurs at the center of the chromosome there would still be room for crossing over at the two ends. That is, triple crossing over involving the center and the two ends should be more frequent than in *D. melanogaster,* where the X chromosome is shorter. This is actually found to be the case. The coincidence of triple crossing over involving the regions sepia crossveinless, crossveinless forked, and Triangle rugose is 0.75, which is higher than the highest value for triple crossing over reported in the X chromosome of *melanogaster.* If the crossveinless forked distance were replaced by a shorter distance at the center of the chromosome the coincidence would probably be still higher—possibly 1.00 or more, which would mean that interference had vanished or become negative.

In this connection it is of interest that two quadruple crossovers were observed in the data given in Table 1, and others have been observed in data not there included. Such crossovers have never been observed in the X chromosome of *melanogaster;* in fact, only two cases have hitherto been found—one for the second chromosome in *D. melanogaster* (Muller, unpublished data) and one for the third (Gowen).

NON-DISJUNCTION IN *Drosophila virilis*

Non-disjunction (Bridges) is an abnormal distribution of chromosomes (and hence of genes) due to the failure of the chromosomes to segregate at the reduction division. In such cases one daughter-cell receives both chromosomes of a pair, the other receives neither. This is termed primary non-disjunction.

When non-disjunction of the X chromosomes occurs, and an egg containing two X's is fertilized by a Y-bearing sperm, an X X Y individual results. When the eggs of this individual are formed, generally the two X's separate in reduction, the Y going with one of them. But in a certain percentage of cases the two X's go to one pole, the Y to the other. This is termed secondary non-disjunction.

In *D. virilis*, where I have been studying primary and secondary non-disjunction, the phenomena seem genetically identical with those in *D. melanogaster* and the behavior of the chromosomes is undoubtedly the same. The rate of secondary non-disjunction in *D. virilis* has been found to be 1.3 per cent (out of 1,511 flies in a non-disjunctional stock, there were 792 regular females, 700 regular males, 8 exceptional females, and 11 exceptional males). This indicates that the rate of secondary non-disjunction in *D. virilis* is somewhat lower than the rate found in other species—4.3 per cent in *D. melanogaster* (Bridges), 2.9 per cent in *simulans* (Sturtevant), 1.7 per cent in *willistoni* (Lancefield and Metz).

I am now measuring the rate of the occurrence of primary non-disjunction and have made up a stock that will render possible the detection of non-disjunction in equational as well as in reduction divisions.

When an egg-cell that has received neither X chromosome is fertilized by an X-bearing sperm, an individual results having one X and no Y. In *D. melanogaster* such individuals are known to be sterile males. In *D. virilis* I have tested a male that resulted from primary non-disjunction. This male produced no offspring although he was mated successively with six different females. If this is representative of primary non-disjunctional males in *D. virilis,* it would indicate that here, as in *D. melanogaster,* the Y chromosome carries one or more factors necessary for fertility in the male. The Y chromosome is not known to carry any other factor in *D. virilis;* in this species, as in *melanogaster,* XXY individuals seem to be females somatically indistinguishable from XX females.

GYNANDROMORPHS

An abnormal distribution of chromosomes may occur in a somatic division with the result that one cell, and all the cells derived from it, may come to have a chromosome complex different from that of the other cells. Individuals in which some cells thus differ from others become mosaics or gynandromorphs.

In the work on *D. virilis,* a gynandromorph was observed which must have resulted from a loss of one of the X chromosomes in the course of development. This gynandromorph was derived from a cross of a female heterozygous for crossveinless by a forked male. The other offspring of the cross were the expected classes (wild-type females, wild-type males, and crossveinless males). In the gynandromorph, the thorax and the scutellum were forked on the right side and wild-type on the left side. Since the forked gene not only affects the bristles but also makes the thorax and scutellum glossy, the line of demarcation between the forked and the not-forked regions was very sharp. The bristles on the head were all forked. The right wing was shorter (a male character) than the left; neither wing was crossveinless. The genitalia were female.

This individual probably began as a female, having received one forked chromosome from the father and one not-forked chromosome from the mother. At an early stage in the development the not-forked chromosome must have been eliminated from one of the cells, so that the regions of the body derived from this cell showed the forked character.

MUTATION

It had originally been planned to utilize the linkage experiment described above for a study of the rate of mutation in *D. virilis.* A measure of the mutation rate may be obtained by noting the frequency of occurrence of sex-linked lethal factors, as has been done by Muller and Altenburg for *D. melanogaster.* The appearance of a lethal in an X chromosome of a female may be detected by a deficit of individuals in those classes of sons that receive the lethal; hence the method cannot be used where some classes are already deficient because of poor viability due to the combinations of genes they contain. Such differential inviability was present in the linkage experiment, and rendered it impossible to use the data for a determination of the rate of occurrence of lethals.

Differential inviability may be decreased by reducing the number of mutant factors used and by decreasing the crowding of larvae in the cultures. This latter can be done by transferring the parents every few days to new culture bottles. These methods will, it is hoped, eliminate the difficulty.

A number of non-lethal mutations have been observed. The inheritance of these is being studied and their loci in the chromosomes are being worked out. The mutations are as follows:

(1) A very short wing resembling the vestigial wing in *D. melanogaster* and, like the latter, an autosomal recessive.

(2) A shortening of the fifth longitudinal vein. An autosomal dominant.

(3) Spread wing. Probably autosomal.

(4) A wing with thickened veins, resembling Confluent, and like it an autosomal dominant. If this turns out to be identical with Confluent or allelomorphic to it, the case will be of interest as a recurrence of a mutation.

(5) A small wing resembling miniature and dusky in *D. melanogaster,* and like them a sex-linked recessive. The locus is about seven units to the left of forked.

Several mutations have also been observed in *D. melanogaster.*

(1) Notch. This is a sex-linked dominant with a recessive lethal effect. It is of interest because of its comparatively frequent occurrence (it has previously been observed about sixteen times) and because it seems to be due to a deficiency of genetic material in the facet locus and sometimes in one or more adjacent mutant loci (Mohr). The deficiency in the present case seems to cover the facet gene (as the facet-Notch hybrids show both characters) but no other genes. In the case of one previous Notch, the hybrids with facet were found to be sterile (Bridges). The hybrids in the present case were tested and proved fertile.

(2) A shortening of the fifth vein. The gene is recessive and located in the third chromosome.

(3) A non-sex-linked recessive (third chromosome) causing a dilution of the eye color apricot. Apricot is an allelomorph of white found by Clausen (unpublished data) and makes the eye color of both sexes about like that of the eosin male. The modifier dilutes the color, making it about as light as eosin ruby. It does not affect the wild-type eye, and its effect on the other allelomorphs is being tested.

The experiments are being continued and additional ones undertaken. It is hoped that further data will help in the solution of the problems under consideration.